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DESERT TORTOISE (*Gopherus agassizii*) REPRODUCTION IN THE MAZATZAL MOUNTAINS, MARICOPA COUNTY, ARIZONA

Final Report

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ABSTRACT

Ten desert tortoises were monitored with radio telemetry between 12 September 1991 and 12 September 1993 to collect baseline reproduction data for Sonoran Desert tortoises. Eggs were detected by palpation in 1992 and by palpation and radiography in 1993. Two of eight tortoises were determined to be gravid in 1992, and eight of 10 in 1993. Radiography revealed that palpation was only 50% effective in 1993. Mean clutch frequency was 0.78 clutches/female, and clutch size averaged 5.7 eggs/clutch/gravid tortoise in 1993. Oviposition occurred before and during the summer monsoon season in both years, from early June to early August. After laying eggs, tortoises remained at a single burrow for several weeks, apparently guarding their nests. Mean corrected home range area was 12.6 ha during the study, but the area utilized differed between years for some tortoises.

INTRODUCTION

Desert tortoise reproductive biology is known primarily from observations of captive animals and from studies in the Mojave Desert (Johnson et al., 1990). No reproduction studies have been reported for Sonoran Desert tortoise populations. These populations differ genetically, morphologically, and ecologically (Lamb et al., 1989; Lowe, 1964; Luckenbach, 1982; Weinstein & Berry, 1987), but data from the Sonoran Desert are needed to compare their reproductive biologies.

Preliminary data gathered in 1992 indicated that Sonoran Desert tortoises lay a single clutch of eggs during late June to early July, in contrast to the multiple clutches reported by Turner et al. (1984, 1986) in the Mojave Desert. Our preliminary data also suggested that Sonoran clutch sizes may be larger than those in the Mojave Desert (Murray and Schwalbe, 1993).

The primary objectives of this study were to collect additional baseline data on female Sonoran Desert tortoise reproductive biology, including nesting habitat; egg-laying dates; and clutch size, frequency, and mass; and to compare these data with those reported from the Mojave Desert. These data are important, necessary steps in constructing a life table for the Sonoran Desert tortoise, which can aid in assessing viability of that population.

METHODS

STUDY SITE

The study site was in the western foothills of the Mazatzal Mountains, about 48 km northeast of Mesa, Maricopa County, Arizona. We did not delineate fixed boundaries for the site, but it was generally bounded by Arizona Highway 87 on the east, Sugarloaf Mountain on the west, Sugarloaf Mountain Road on the south, and a northeast to southwest running canyon about 2.5 km north of Sugarloaf Mountain Road (Fig. 1).

Vegetation at the study site (hereafter referred to as Sugarloaf) is classified in the paloverde-mixed cacti series (Brown et al., 1979) in the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown, 1982). Arroyos dividing many steep, rocky slopes characterize the topography; boulders up to 4 m diameter occur on the slopes. Rainfall was measured from 5 April 1992 to 12 September 1993 with an all-weather rain gauge (Productive Alternatives, Inc.; from Forestry Suppliers, Inc., Jackson, Mississippi) placed on the saddle of a ridge in the northern section of the study site.

TELEMETRY

Ten adult female tortoises were monitored by radio telemetry between 12 September 1991 and 12 September 1993. Eight Wildlife Materials, Inc. (Carbondale, Illinois) transmitters (model HLPB-2114-MVS) and two AVM Instrument Company, Ltd. (Livermore, California) transmitters (model P2) were mounted to the anterior carapaces of the tortoises.

The Wildlife Materials transmitters were mounted and epoxied with 5 Minute Epoxy Gel (Devcon Corp., Danvers, Massachusetts) into stainless steel brackets which were themselves epoxied to the carapace across the right or left first costal and first vertebral scutes. The antenna slid into a plastic tube epoxied to the left costal scutes. Scute sutures were not epoxied, and the bracket and antenna tubing were cut at each suture to allow for uninhibited growth during the study. The AVM transmitters were bolted to a brass plate epoxied to the left first costal scute instead of being mounted into a bracket. A Wildlife Materials, Inc. TRX-2000S receiver and collapsible Yagi antenna were used to locate the tortoises.

Each telemetered tortoise was also assigned an identification number; marginal scutes were notched accordingly with a triangular file, using the coding system developed by Ernst et al. (1974). Tortoises were weighed with Pesola spring scales (Forestry Suppliers, Inc.); median carapace length (MCL) was measured with calipers and a metric rule.

Five female tortoises were originally fitted with transmitters on 12-13 September 1991. One of the original females lost her transmitter during the first month, and new females were fitted with transmitters on 26 October, 2 November, 22 and 28 March, 15 June 1992, and 10 July 1993. We continued to monitor these ten females until 12 September 1993, at which time all transmitters and brackets were removed.

Home range areas were estimated with the minimum convex polygon method included in the software package McPAAL, Version 1.2 (Stuwe and Blohowiak, undated). We applied Jennrich and Turner's (1969) sample size bias correction factor to the measured area estimates following Barrett (1990):

$$\text{Corrected Home Range} = \frac{\text{Measured Home Range}}{0.257 \ln(\underline{n}) - 0.31},$$

where ln ($\underline{n}$) is the natural logarithm of the number of observations (n). Yearly activity ranges were estimated for 1992 and 1993, observations included in the calculations beginning with exit from hibernation for each tortoise. The last date included was in the fall when any tortoise made an obvious long-distance movement away from its summer activity area; thus, any seasonal shifts in activity areas were standardized between tortoises. Overall home ranges were estimated by including all mappable observations for each individual.

REPRODUCTION MEASUREMENTS

We monitored tortoises at least weekly from mid September 1991 to October 1992, recording weights each time they were located outside or when they could be retrieved from their burrow. Gravid tortoises were determined in 1992 by palping anterior to the rear legs for presence of eggs. Straight-line distances between consecutive captures were measured with a range-finder when possible, and estimated otherwise.

We radiographed the tortoises in the field between 12 June and 12 September 1993 with a MinXray 210 portable X-ray machine (13 mA and 66 kV peak) powered with a Honda gasoline generator. Tortoises were carried in clean cotton pillow cases from their point of capture to the X-ray machine at the vehicle and usually returned to the point of capture within an hour. The X-ray machine was mounted on a tripod, with the X-ray source 71.1 cm above the radiograph cassettes. We used rare earth intensifying cassettes and Kodak Ektascan M film with a 0.5-sec exposure or Fuji Medical RX-U film with a 0.4-sec exposure. Radiographs were developed with an automatic processor at the Arizona Health Sciences Center. Entrance shell radiation doses (ESD) were calculated for each tortoise according to the formula,

$$ESD = \text{Time (in sec.)} * 13\ \text{mA} * 7.6\ \text{mr/mas} * 1.42,$$

and summed for the entire study (Univ. of Arizona, Radiation Control). We determined palpation efficacy by comparing palpation and radiograph results. All means are presented $\pm$ 1 standard error (SE). We compared Sugarloaf results with those published by Turner et al. (1986) from Goffs, California, with the Mann-Whitney U-test and Tukey's test (Zar, 1984). In order to maintain independence among individuals from Goffs, we averaged values for each individual across years for clutch frequency and overall for clutch size before making statistical comparisons.

RESULTS

Two of eight (25%) telemetered adult female tortoises were determined by palpation to be gravid in 1992. Tortoise #4 laid eggs between 15-24 June (210 g weight loss); tortoise #19 laid eggs between 24 June and 2 July (452 g weight loss) (Fig. 2; Appendices 1-2). No eggs were detected in any tortoise after the end of June in 1992. We used these results to schedule field radiography in 1993. Appendices 1-4 contain weight data relative to rainfall for 1992 and 1993.

CLUTCH SIZE AND FREQUENCY

Radiography revealed that seven of the 10 telemetered tortoises were gravid in 1993; another tortoise (#21) laid eggs (determined by the presence of eggshell fragments in her burrow on 12 December) before the initiation of radiography (Table 1). Tortoises received a mean cumulative ESD of 424.85 $\pm$ 32.17 mRads (224.4 - 546.8) during the study. Eggs were initially detected by palpation in only four of the eight gravid tortoises (50%) in 1993. Failure to detect eggs by palpation appeared to be due to small clutches in early development (tortoise #1), tight shell closure preventing effective palpation (tortoise #12), or both of the above (tortoise #4).

Mean clutch frequency (total number of clutches divided by all females; tortoise #33 was excluded since she was not monitored during the entire oviposition period) was 0.78 clutches/female (SE = 0.147; n = 9); no tortoise laid more than one clutch. Clutch sizes ranged from 3-9 eggs ($\bar{X}$ = 5.7 $\pm$ 0.92) per clutch per gravid female at Sugarloaf (Table 1).

OVIPOSITION

Oviposition occurred between 6 June and 7 August 1993 (Fig. 2; Appendices 3-4). Tortoise #33 likely laid eggs earlier than 7 August, but she could not be retrieved from her burrow for radiography during the intervening visit on 24 July. Oviposition generally occurred just before and during the beginning of the summer monsoon season (Fig. 2).

We verified three nests between 1992 and 1993. In 1992, tortoise #4 laid eggs in a 38 cm deep burrow, with an aspect of 296 degrees, in sandy soil below a jojoba (*Simmondsia chinensis*), with red brome (*Bromus rubens*) and *Vulpia* sp.; slope was approximately 30%, facing north (13 degrees). In 1993, tortoise #19 laid eggs in a 35 cm deep burrow, with an aspect of 290 degrees, in soil and exfoliated granite at the base of a granitic boulder (approximately 0.5 m diameter); slope was approximately 25%, facing north (349 degrees). Tortoise #21 laid eggs in a 75

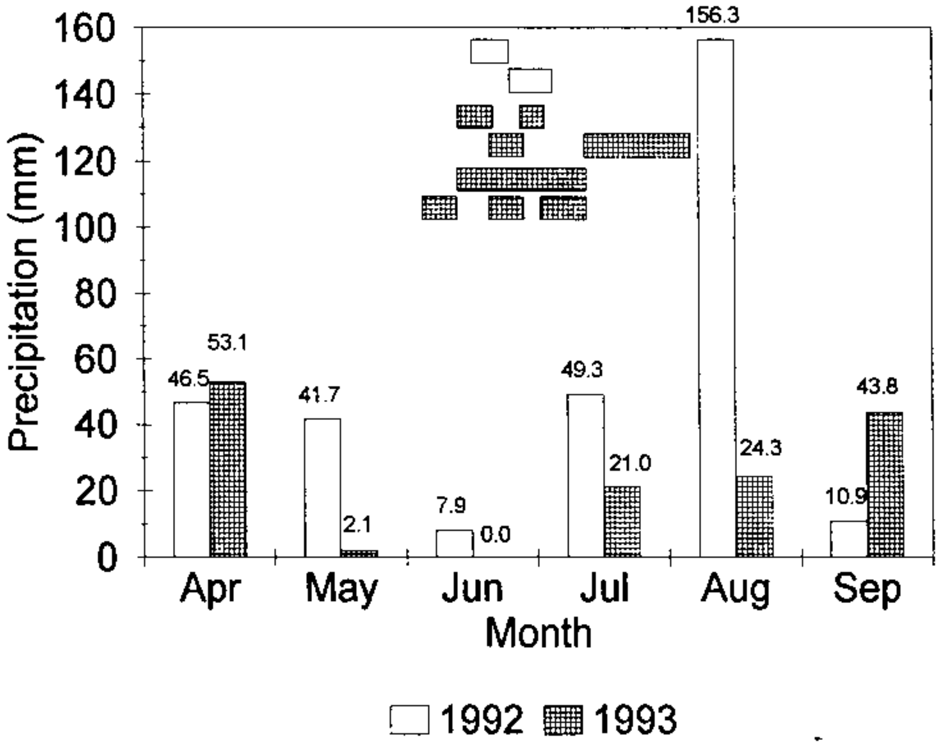

Fig. 2.--Oviposition in desert tortoises at Sugarloaf in relation to monthly precipitation totals. Horizontal bars represent time periods during which individual tortoises laid eggs.

Table 1.--Desert tortoise clutch sizes at Sugarloaf, Tonto National Forest, Maricopa County, Arizona in 1993. MCL = median carapace length. Numbers indicate clutch sizes determined by radiography; weight changes after oviposition or at initiation of radiography are indicated in parentheses; underlining indicates clutches (dashed indicates uncertainty of oviposition).

Tortoise number	MCL (mm)	June 12-13	June 19-20	June 26-27	July 1	July 10-11	July 24-25	August 7-8	August 21-22	Sept 11-12
01	244	3	3	P	0^P (-100g)	0	0	0	0	0
04	243	3	3	0 (-150g)	*	0	0	0	0	0
12	220	6	?	?	?	0 (-380g)	0	0	0	0
13	220	0 (-20g)	?	0^P	*	0	?	?	0	0
14	249	0 (+20g)	0	0^P	*	0	0	0	0	0
17[§]	250	4	4	P	P	0 (-190g)	0	0	0	0
18[§]	243	7	P	0^P (-300g)	*	0	0	0	0	X
19[§]	260	9	0 (-340g)	0^P	*	0	0	0	0	0
21	254	0[†] (-200g)	0	0^P	*	0	0	0	0	0
33[§]	260	--	--	--	--	8	?	0 (+160g)	0	0

P = eggs felt by palpation, radiographs not taken.
0^P = no eggs detected by palpation, radiographs not taken.
* = no observation for that date.
? = tortoise could not be retrieved from its burrow.
[§] = eggs felt by palpation on first attempt.
X = film not exposed.
[†] = oviposition occurred before radiography was initiated.

cm deep soil burrow below a granitic boulder slab on a north-facing slope of approximately 25% grade.

NEST DEFENSE

Tortoises known to have laid eggs tended to remain at a single burrow following oviposition (Appendices 5-6). Since we only verified three nests, we cannot state conclusively that post-gravid tortoises were guarding their nests, but this behavior has been reported in the literature (Barrett and Humphrey, 1986). The following circumstantial evidence does indicate that Sugarloaf tortoises may have been guarding nests.

Behavioral observations suggested that tortoise #21 laid eggs in 1993 even though she was not gravid when we began field radiography on 12 June. She had lost 200 g during the week prior to radiography (Table 1) and was found in a burrow which she did not leave until 7 August (Appendix 6). She was very defensive of this burrow during the intervening observations and moved to the mouth of the burrow at the slightest disturbance (including the sight or sound of observers approaching), blocking the entrance. On 12 December, we verified oviposition in this burrow by the presence of eggshell fragments in and around the burrow entrance.

Tortoise #17 behaved similarly in 1992, even though she was not determined to be gravid by palpation; from 2-9 June she moved an estimated 625 m to a new burrow (Appendix 5) and lost 274 g between 2-15 June. She was found at her 15 June burrow until 22 September and readily came to the entrance when her carapace was tapped.

Tortoise #1 (no eggs detected by palpation) stayed in the same burrow from 2 July to 22 August 1992 (Appendix 5), but could not be retrieved during most visits. In addition, most of the other tortoises determined by radiography to be gravid in 1993 were not defensive toward observers. Tortoises #4 and 19 (eggs detected by palpation) in 1992, and tortoise #33 (eggs detected by radiography) in 1993, did not remain long at the same burrow after laying (Appendices 5 and 6, respectively).

MOVEMENTS AND HOME RANGE

Movements between observations were recorded throughout the study, but statistical comparisons of movements in 1992 were not made due to the inefficacy of palpation in detecting eggs. The logistics of this project required volunteers to assist in locating tortoises, bringing them to the X-ray machine, and returning them to their point of capture. Field assistants were often unfamiliar with previous tortoise locations, resulting in incomplete movement data between observations. This precluded statistical analyses of movements in 1993.

Corrected home ranges ranged from 2.3-50.7 ha ($X = 12.6 \pm 4.98$ ha, excluding tortoise #33 because of only five observations) from 12 September 1991 to 12 September 1993 (Table 2); polygons are shown in Figs. 3-5. However, activity areas differed greatly between years and seasons for some tortoises. Tortoise #12 occupied a 13.3 ha area in 1992, north of her 1991 capture location, before moving about 1 km to the east by 30 October 1992 (Table 2, Fig. 4). She then occupied a 15.0 ha area during 1993 before moving back toward and south of her 1992 activity area in late summer 1993 (Table 2, Fig. 4). Even though tortoise #33 was only located five times, she also appeared to be making a seasonal movement away from her summer activity area on 12 September 1993; she had moved about 1/2 km southwest and was moving in that direction when located (Fig. 3).

Tortoise #17 occupied the same 0.8 ha area in both years, but she moved about 3/4 km to the north by 9 June 1992 and stayed in the same burrow (and possibly laid eggs) until 19 September 1992 (Table 2, Fig. 5). The remaining tortoises occupied the same general areas in each year, but Tortoise #13 spent more time in the southern end of her home range in 1992 (Figs. 3-5).

Mean home range size appeared to be smaller in 1993 than in 1992 (Table 2), but this was not tested statistically because of differences in sample sizes between years. Estimated home range area often increases with sample size (Macdonald et al., 1980), but the drier summer in 1993 (Fig. 2) may have resulted in smaller home range areas due to decreased activity.

Table 2.--Corrected minimum convex polygon home range areas (ha) for adult female tortoises at Sugarloaf. Sample size (n; # of observations) is included in parentheses. 1992 and 1993 home ranges do not include hibernacula. Total home range includes all mappable observations for each individual.

Tortoise number	Home Range (n) 1992	1993	Total
01	2.4[a] (33)	0.8[b] (15)	3.2 (62)
04	5.5[a] (32)	2.2[b] (14)	4.9 (59)
12	13.3[a] (31)	15.0[b] (15)	50.7 (59)
13	10.4[a] (26)	2.3[c] (11)	9.2 (50)
14	5.7[a] (30)	3.7[d] (13)	5.0 (52)
17	10.9[a*] (34)	0.8[b] (15)	9.0 (58)
18	2.5[a] (26)	1.4[b] (14)	2.3 (44)
19	14.0[a] (29)	1.4[b] (14)	14.1 (47)
21	17.9[e] (16)	9.2[b] (14)	14.7 (31)
33	---------	4.3[f] (4)	15.4 (5)
Mean (excl. #33)	9.2 (SE=3.70)	4.1 (SE=1.62)	12.6 (SE=4.98)

[a] 5 Mar - 5 Oct 1992. Truncated at 5 Oct due to long-distance movement by Tortoise #12 away from summer activity area.

[b] 12 Mar - 22 Aug 1993. Truncated at 22 Aug due to long-distance movements by Tortoises #12 and 33 away from summer activity areas.

[c] 7 Apr - 21 Aug 1993.

[d] 23 Mar - 22 Aug 1993.

[e] 15 Jun - 4 Oct 1992.

[f] 10 Jul - 21 Aug 1993.

* = used the same burrow most of summer (9 Jun - 19 Sep) away from normal activity area.

DISCUSSION

CLUTCH SIZE AND FREQUENCY

The lack of large decreases in body masses during both springs indicate that Sugarloaf tortoises did not lay eggs before the summer laying period (Appendices 1-4). Sugarloaf clutch frequency differs from those reported by Turner et al. (1986) for Mojave Desert tortoises at Goffs, California, from 1983-1985. They reported that all but one of the females under observation laid eggs, with frequencies ranging from 0-3 clutches/tortoise (means of 1.89 $\pm$ 0.105 [n = 19], 1.57 $\pm$ 0.123 [n = 23], and 1.75 $\pm$ 0.123 [n = 20] clutches/female/year from 1983-1985, respectively). The typical Mojave pattern was one or two clutches laid in May and June; there was a significant relationship between mean clutch frequency and net annual plant production, which is related to winter rainfall (Turner et al., 1986). Clutch frequency is significantly greater for the pooled Goffs data (1.69 $\pm$ 0.099; n = 30) when compared to Sugarloaf with the Mann-Whitney U-test (P = 0.0001).

Mean clutch size at Sugarloaf was not significantly different from that at Goffs (1983-1985 X = 4.3 $\pm$ 0.19 eggs/clutch; range = 1-8) when compared using the Mann-Whitney U-test (P = 0.2228). However, this conclusion is tenuous due to the small sample size at Sugarloaf (n = 7) compared to Goffs (n = 29). Tukey's test indicated that Sugarloaf tortoises laid significantly fewer eggs (total number of eggs divided by all females) (4.4 $\pm$ 1.09 eggs/year) than did Goffs tortoises in 1983 (7.8 $\pm$ 0.61) and 1985 (9.0 $\pm$ 0.70), but not in 1984 (6.7 $\pm$ 0.64).

If female reproductive investment is similar between populations, one would expect larger or heavier clutches in the Sonoran Desert, if Sonoran tortoises only nest once a year. More data are needed to more rigorously compare the two populations. Two additional pieces of anecdotal evidence suggest that the Sonoran Desert population may produce larger clutches than the Mojave population: an adult female (278 mm MCL) taken from an ASARCO mine mitigation project in Pima Co., AZ (C. Gruenwald, pers. comm.) laid 12 eggs in captivity between 18-24 June 1992, and a female (252 mm MCL) near Arizona Game and Fish Department's Little Shipp permanent monitoring plot in Yavapai County, was found to have 11 eggs (C. Klug, pers. comm.).

NEST DEFENSE

Differences in tortoises remaining at nest sites may possibly be attributed to the amount of previous handling, as well as individual variation. Handling (extraction from burrows, weighing, palpation, and transport to and from the radiography station) may have disturbed some tortoises enough to leave their nests. The two tortoises known to be gravid in 1992 (#4 and 19; Appendix 5) and the newest tortoise in 1993 (#33; Appendix 6) had only recently been captured and fitted with transmitters and were not accustomed to being handled by researchers. However, the first seven gravid tortoises in 1993 had been extracted, weighed, and palped during each observation for a year or more (excluding winter hibernation). These tortoises may have become conditioned to this treatment, and therefore did not leave their burrows after laying.

The two tortoises previously suggested to have laid eggs, but not confirmed, in 1992 (#17 and #1) may have remained at nest sites because of other factors. We were not able to extract tortoise #1 from her burrow between 15 June and 3 August 1992 (Appendix 1), so she was not handled during the time she would have been guarding her nest. Tortoise #17 was a very aggressive individual that readily confronted researchers at her burrow, so handling apparently had little effect on her behavior.

If nest defense behavior is common, there may be important ramifications for monitoring population plots. The repeated visitation of areas of high tortoise density and frequent handling of post-gravid females could result in tortoises leaving nests undefended, subjecting them to higher predation rates. Unlike the tortoises in this study (monitored year-round for two years), tortoises on population plots are unlikely to become accustomed to handling, because they are only subject to disturbance for a period of two to three months during a year. Systematic plot coverage (as described in Murray, 1993) and reduced handling (e.g., by limiting physical processing to recording MCL and weight and notching the carapace) would limit the amount of disturbance to individual tortoises during capture occasions.

HOME RANGE

Mean corrected overall home range size for Sugarloaf females (12.6 ± 4.98 ha) is intermediate to those reported for populations in the San Pedro Valley in the western foothills of the Galiuro Mountains, Pinal County, Arizona (2.6 ± 1.2 ha; Bailey, 1992) and the Picacho Mountains, Pinal County (15.3 ± 5.5 ha; Barrett, 1990). Bailey (1992) suggested that better developed soils and denser vegetative ground cover allowed tortoises to obtain the food and shelter necessary for survival and reproduction in smaller areas at his study site. The habitat at Sugarloaf is more similar to that at the Picachos, so it is not surprising that Sugarloaf home range areas are more similar to those at the Picachos.

It should be noted that these estimated home range areas are based on a flat surface; they do not include topographic relief in the estimates. Areas estimated with the minimum convex polygon method may also include unused habitat, resulting in overestimation of home range size (e.g., tortoise #12, Fig. 4). Therefore, conclusions drawn from comparisons between sites (and even between years at the same site) should remain tentative. The main utility in home range estimation lies in the examination of spatial and temporal differences in activity areas relative to habitat use (e.g., tortoise #12 between 1992 and 1993).

SUMMARY AND CONCLUSIONS

Female desert tortoises at Sugarloaf may not reproduce every year, as indicated by the mean clutch frequency of 0.78 clutches/female/year. Mean clutch size was 5.7 eggs/clutch/gravid female and was not significantly different from clutch sizes reported from the Mojave Desert (Goffs, California). Therefore, due to multiple clutching at Goffs, total yearly reproductive output appears to be less for Sugarloaf females than those in the Mojave Desert. However, strong inferences from these results are premature due to the limited amount of data for Sonoran tortoises compared to Mojave tortoises. Anecdotal evidence indicates that Sonoran clutch sizes can exceed the largest recorded in this study.

Oviposition occurred before and during the beginning of the summer monsoon season. Nests were laid inside the burrow entrance, and some females appeared to remain at and guard their nests for several weeks after laying. Researcher disturbance may have caused relatively recently telemetered tortoises to abandon their nests, while "experienced" tortoises (those handled up to six times a month for a year or more) became accustomed to handling. This suggests that the current method of intensively surveying certain areas within permanent population monitoring plots, which results in frequent recaptures of some individuals, may cause females to abandon their nests, subjecting them to predation. Systematic plot coverage and reduced handling would limit disturbance to tortoises during capture occasions.

During the two years of the study, home range areas averaged 12.6 ha, which is intermediate to those reported for Sonoran populations at the Picacho Mountains and the San Pedro Valley. Home range estimates for Sonoran Desert tortoises are extremely coarse due to the complex topography of the habitat, but examination of spatial and temporal differences in activity areas may provide information regarding habitat use. Patterns in actual areas used by tortoises at Sugarloaf varied among individuals; some tortoises occupied separate activity areas between and within years, and some remained in a relatively small area throughout both years.

Further study is needed to better understand desert tortoise reproductive biology; additional data from Sonoran populations will facilitate more rigorous comparisons between tortoises in the Sonoran and Mojave Deserts. More intensive study is also needed to determine nest-site characteristics and clutch survivorship, as well as relationships between egg production and rainfall and plant production in the Sonoran Desert.

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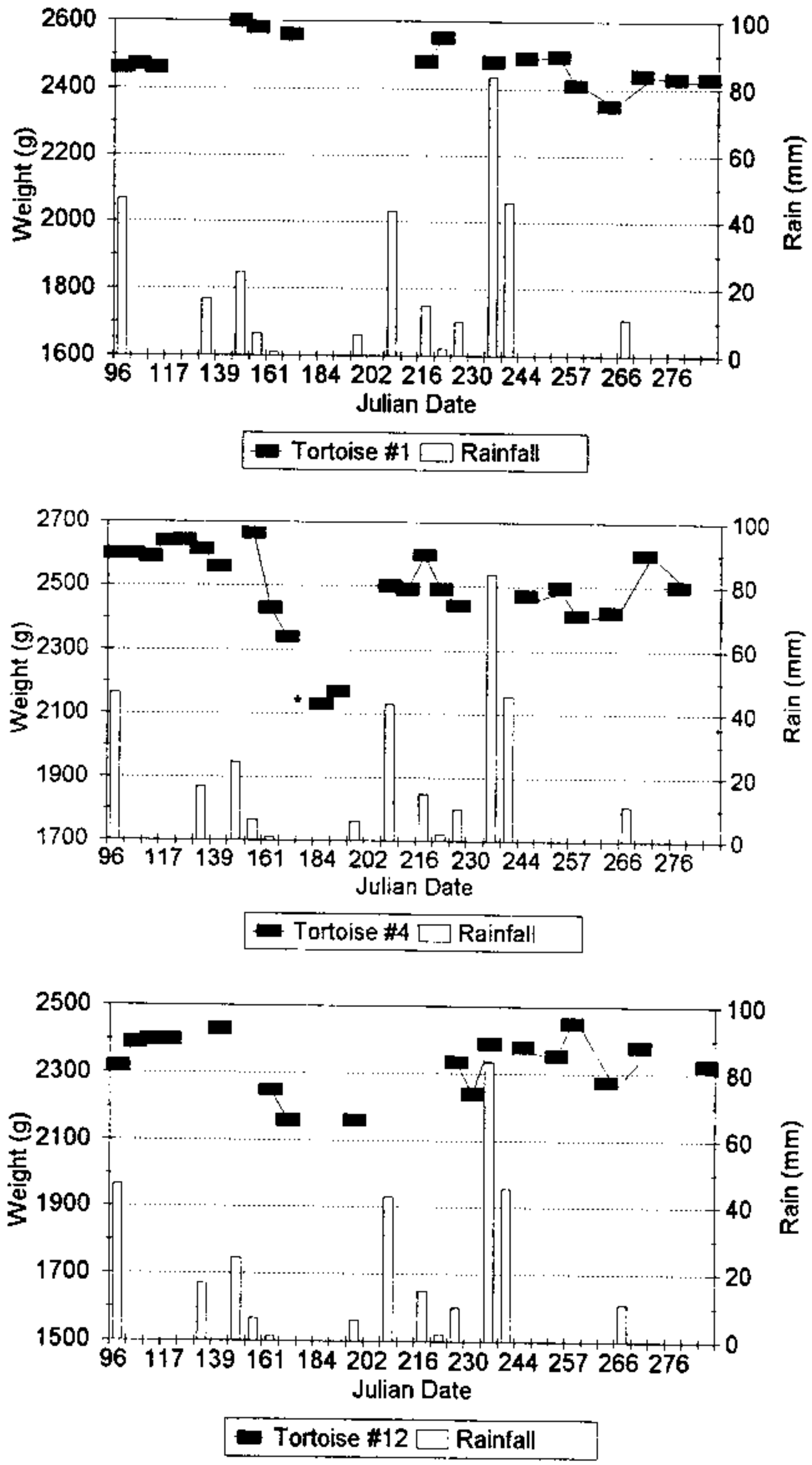
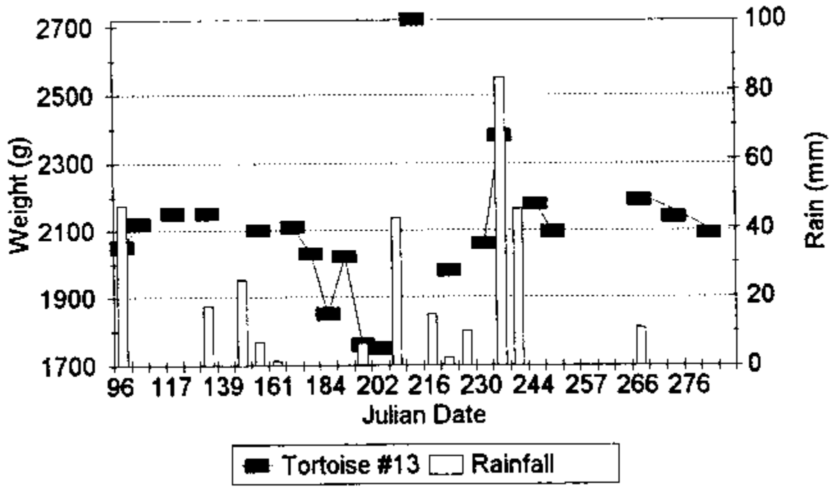
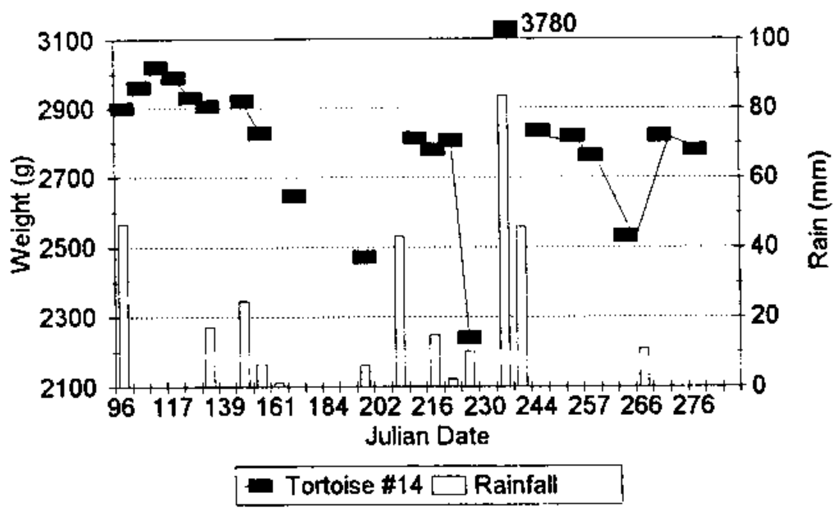
Appendix 1.--Desert tortoise weights and rainfall during 1992 at Sugarloaf. Boxes indicate oviposition windows, with egg-laying occurring after the initial weight in each box; X indicates individuals not located during that trip. Empty cells indicate the tortoise could not be retrieved from its burrow; * indicates first capture.

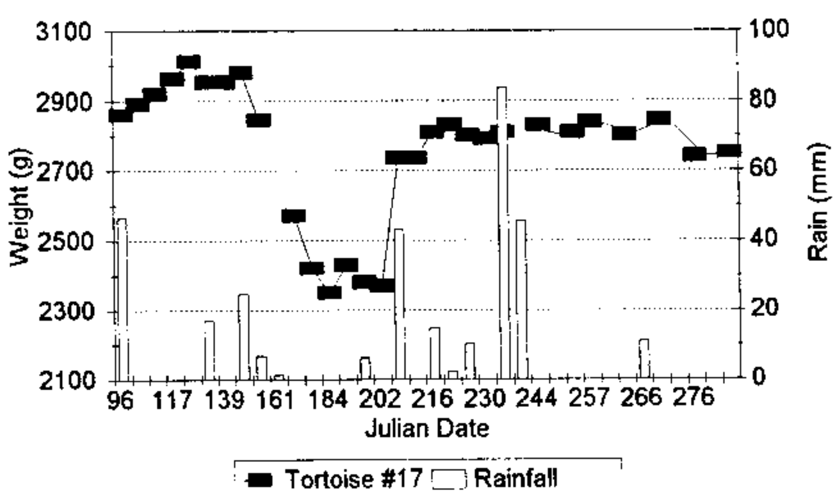
	Rainfall	Weight (g)								
Date	(mm)	#1	#4	#12	#13	#14	#17	#18	#19	#21
29-Feb		2550	2510	2450	2130	2990	2650			
05-Mar		2560	2510		2200		2890			
12-Mar		2490	2600	2500	2020	2890	2800			
22-Mar		2500	2580	2420			2850	2540*		
28-Mar		2550	2600		1960	2900		2450	3050*	
05-Apr	46.5	2460	2600	2320	2050	2900	2860	2370	3060	
12-Apr	0.0	2470	2600	2390	2120	2960	2890		2960	
19-Apr	0.0	2460	2590	2400		3020	2920	2510	3260	
26-Apr	0.0		2640	2400	2150	2990	2962			
03-May	0.0		2642			2930	3011			
11-May	17.0	2612	2614		2150	2905	2952	2650	3142	
18-May	0.0		2559	2430			2952	2560	3080	
26-May	24.7	2600	X	X	X	2920	2980	X	X	
02-Jun	6.7	2580	2665		2100	2828	2845	2450	3280	
09-Jun	1.2		2430	2250						
15-Jun	0.0	2560	2340	2160	2110	2645	2571		3214	2945*
24-Jun	0.0	X	.		2030	X	2420		3080	2750
02-Jul	0.0		2130		1850		2350		2628	
06-Jul	0.0		2170		2020		2430		2679	2580
15-Jul	6.3			2160	1760	2470	2380		2870	
20-Jul	0.0				1750		2370	2420		2842
25-Jul	43.0	X	2500	X		X	2735	X	2875	X
29-Jul	0.0		2490		2720	2812	2735	2720	3055	2820
03-Aug	14.8	2480	2597			2780	2810	X	3180	3010
08-Aug	2.2	2550	2490		1980	2805	2830	X		2830
12-Aug	10.1		2440	2335		2240	2800	X		X
17-Aug	0.0			2240	2060	X	2792	2745	3140	X
22-Aug	83.6	2480	X	2390	2380	3780	2810	2825	3240	2790
25-Aug	45.6									
31-Aug	0.0	2490	2470	2380	2180	2835	2830	2660		2940
06-Sep	0.0				2095			2645	3170	2905
07-Sep		2495	2495	2355		2820	2810			
13-Sep	0.0	2410	2410	2450		2762	2840	2582	3168	2918
18-Sep	0.0								3210	2800
19-Sep		2350	2420	2275		2530	2800			
22-Sep	10.9				2190			2700	3340	3010
23-Sep		2440	2600	2380		2820	2845			
01-Oct	0.0				2140					
02-Oct		2430	2500			2780	2740			
04-Oct					2090					
05-Oct		2430		2325			2750			



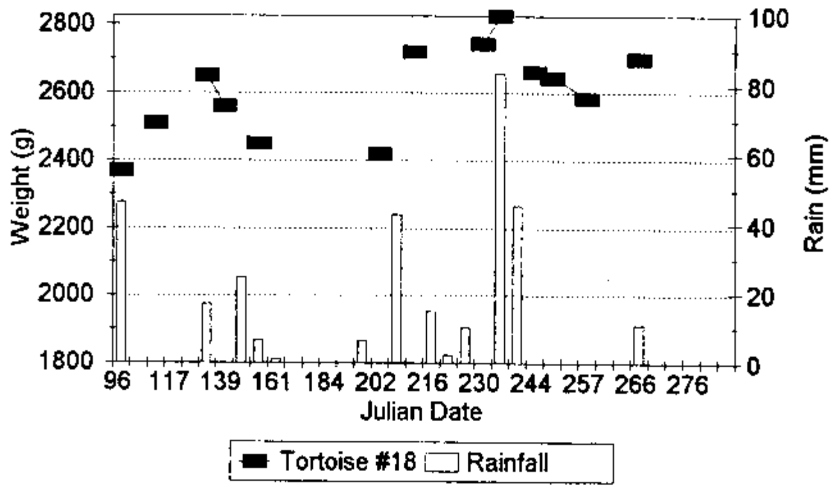
Appendix 2.--Desert tortoise weights and rainfall at Sugarloaf, 5 April - 5 October 1992. Asterisks indicate oviposition had occurred since previous weight record; lines connect consecutive weight records; missing lines indicate inability to extract tortoise from burrow to weigh during intervening trips.

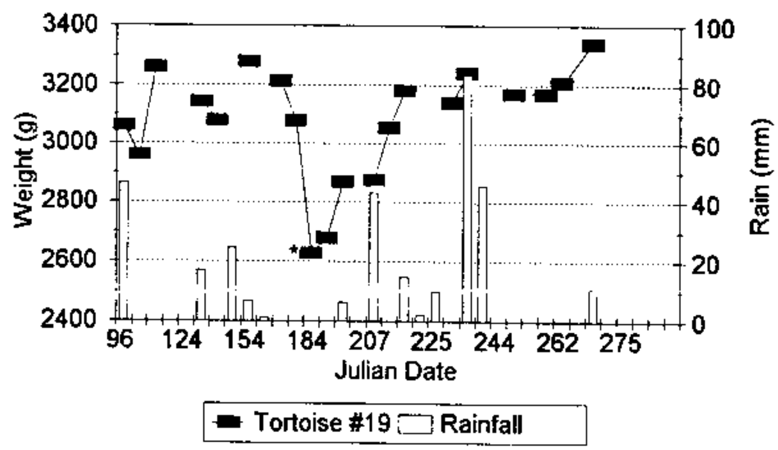


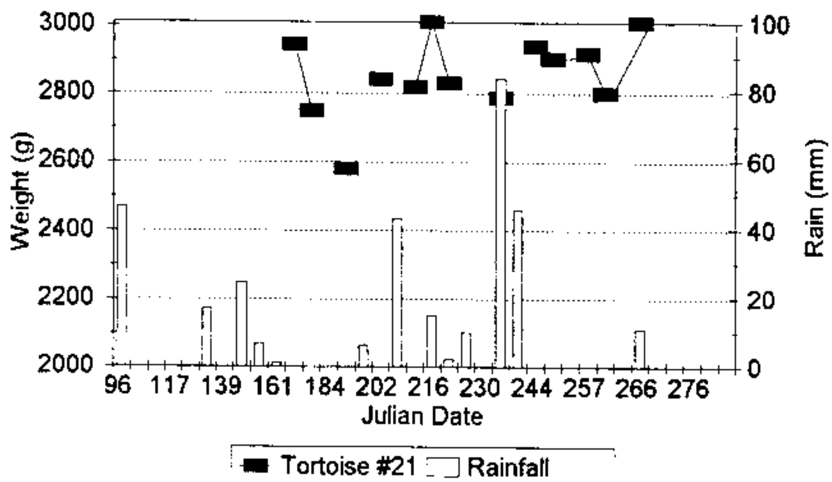




Appendix 2.--continued.



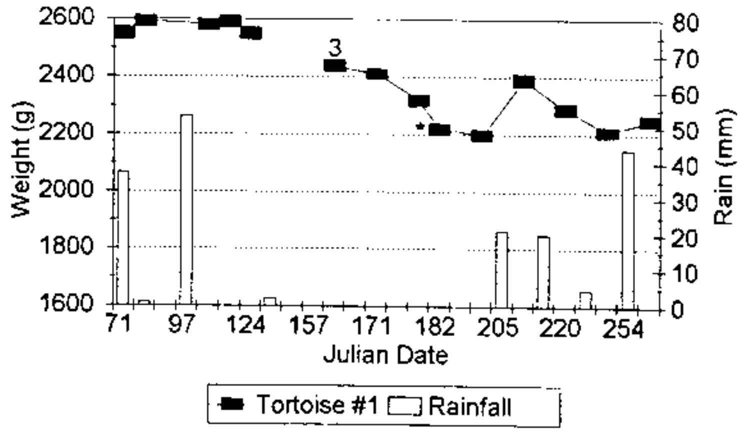


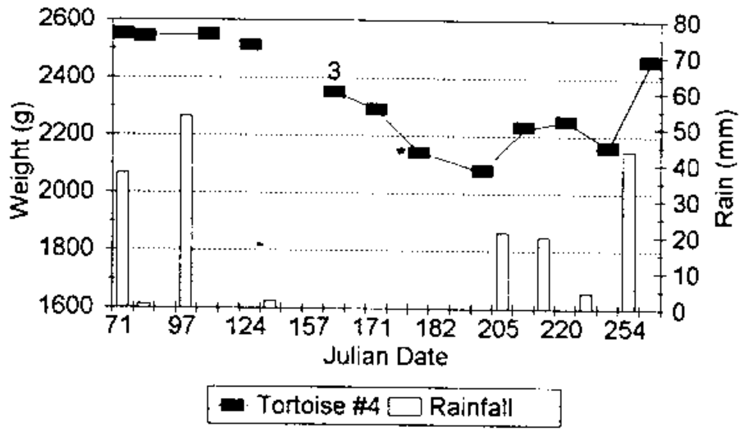


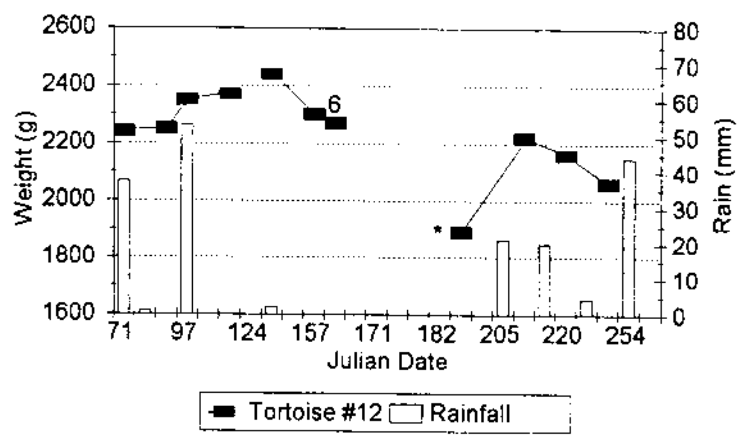
Appendix 2.--continued.

Appendix 3.--Desert tortoise weights and rainfall during 1993 at Sugarloaf. Boxes indicate oviposition windows, with egg-laying occurring after the initial weight in each box; X indicates an individual not located during that trip. Empty cells indicate the tortoise could not be retrieved from its burrow; * indicates first capture.

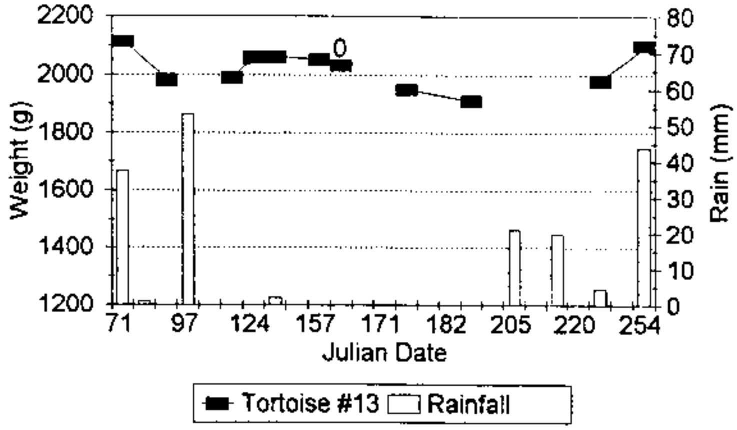
	Rainfall	Weight (g)									
Date	(mm)	#1	#4	#12	#13	#14	#17	#18	#19	#21	#33
12-Mar	37.4	2550	2550	2240	2110		2950	2650	3250	2950	
23-Mar	1.001	2590	2540			2750	2800				
24-Mar				2250	1980			2650	3250	2940	
07-Apr	53.1			2350				2650		2950	
08-Apr		2580	2550			2740	2720				
17-Apr	0.0	2590		2370	1990	2800	2850	2710		2920	
04-May	0.0	2550	2510		2058		2890		3290	2920	
19-May	2.1			2440	2060			2600	3280	2950	
20-May							2800				
06-Jun	0.0			2300	2050	2760	2800	2520	3200	2800	
12-Jun	0.0	2440	2350	2270	2030	2780	2790	2510	3150	2600	
19-Jun	0.0							2500	2810	2560	
20-Jun		2410	2290			2670	2540				
26-Jun	0.0				1950			2200	2720	2580	
27-Jun		2320	2140			2600	2460				
01-Jul		2220	X		X	X	2410	X	X	X	
10-Jul	0.0			1890	1910			2140	2750	2490	2790*
11-Jul		2200	2080			2400	2220				
24-Jul	21.0							2590	2800	2725	
25-Jul		2390	2230	2220		2600	2300				
07-Aug	19.9							2440	2950	2700	2910
08-Aug		2290	2250	2160		2680	2320				
21-Aug	4.4				1980			2600	2720	2650	2950
22-Aug		2210	2160	2060		2590	2190				
11-Sep	43.8				2100			2450	3150	2950	3000
12-Sep		2250	2460			2600	2620				

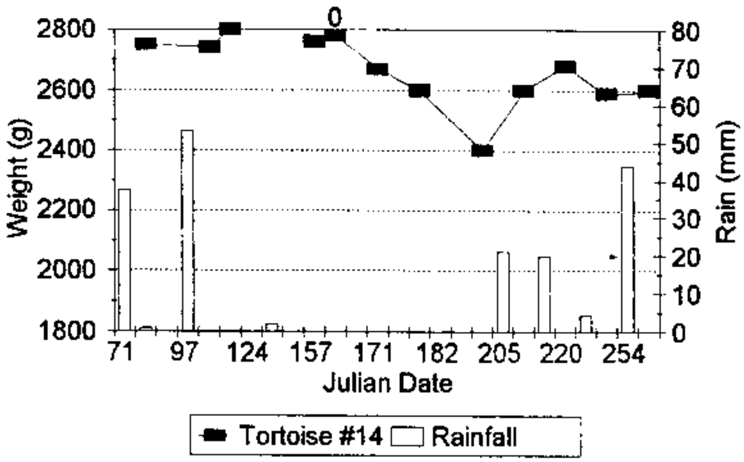


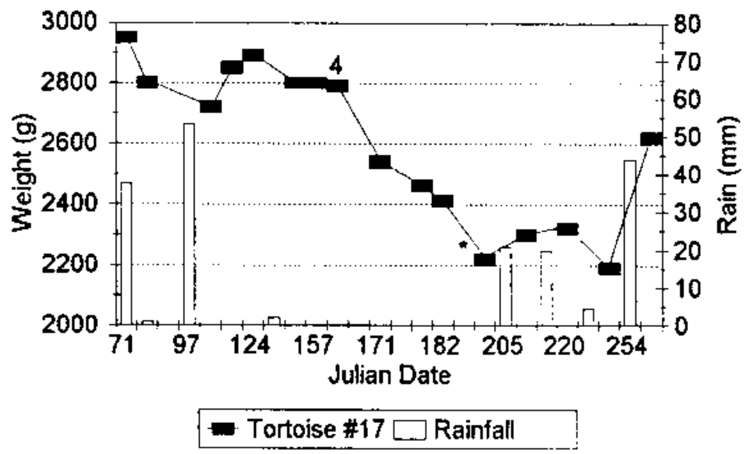




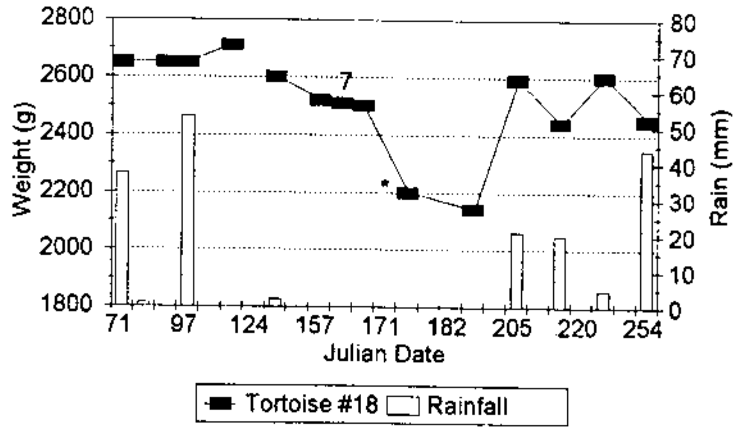
Appendix 4.--Desert tortoise weights and rainfall at Sugarloaf, 12 March - 12 September 1993. Numbers in line graph indicate clutch size determined by radiography; asterisks indicate oviposition had occurred since previous weight record; lines connect consecutive weight records; missing lines indicate inability to extract tortoise from burrow to weigh during intervening trips.

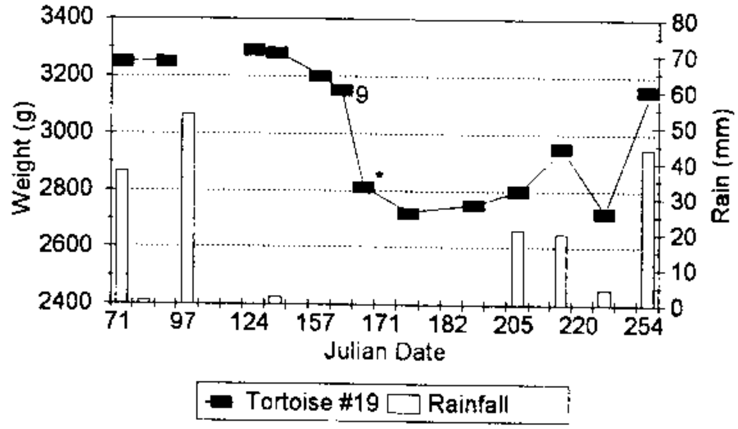


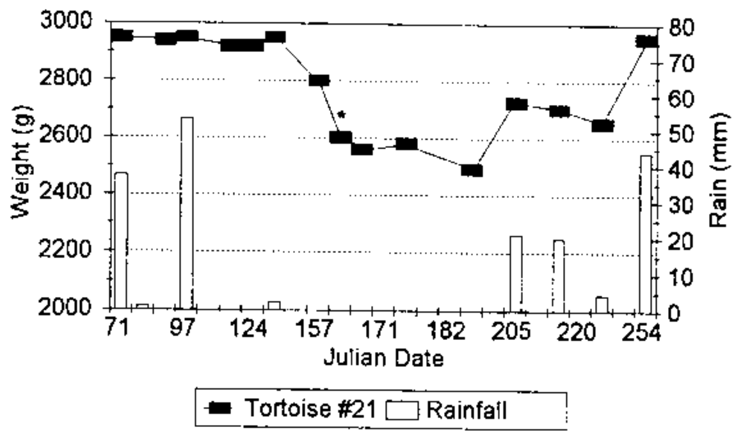




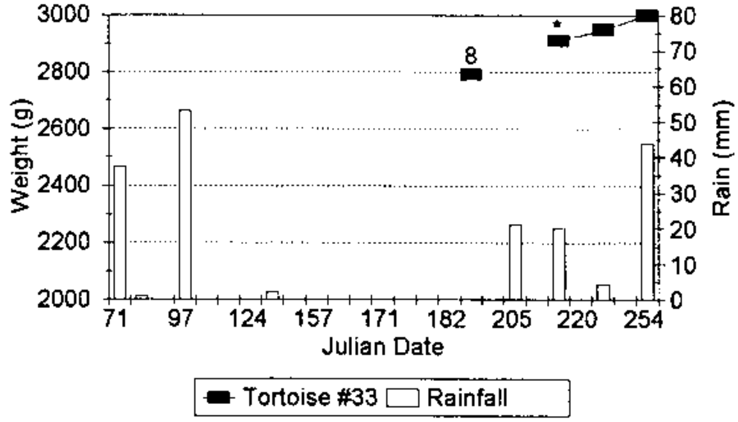
Appendix 4.--continued.







Appendix 4.--continued.



Appendix 4.--continued.

Appendix 5.--Distances moved by desert tortoises between observations in 1992. Brackets indicate oviposition windows; dashes indicate undetermined movement distance (>0 m); X indicates tortoise not located on that visit; asterisks indicate estimated distances.

	Distance moved (m)								
Date	04	19	01	12	13	14	17	18	21
5 Apr	80*	67	19	---	70*	89	80*	68	
12 Apr	80*	200*	31	---	120*	89	90*	68	
19 Apr	64	150*	50*	---	250*	100*	37	0	
26 Apr	65*	0	15*	100*	50*	150*	35*	70*	
3 May	90*	0	30*	20	250*	10*	75*	40*	
11 May	55	150*	9	0	20*	60*	40*	20*	
18 May	80*	150*	9	75*	10	120*	125*	70*	
26 May	X	X	150*	X	X	100*	140	X	
2 Jun	130*	150*	52	220*	200*	120*	34	200*	
9 Jun	100*	120*	55	200*	200*	45	625*	200*	
15 Jun	150*	175*	55	400*	100*	80*	0	20	New
24 Jun	---	200*	X	X	150*	X	0	11	51
2 Jul	21	700*	55	200*	60	---	0	11	70*
6 Jul	0	0	0	0	350*	0	0	0	10
15 Jul	47	100*	0	100*	100*	100*	0	39	9
20 Jul	0	0	0	0	100*	0	0	0	---
25 Jul	---	---	X	X	60*	X	0	X	X
29 Jul	50*	200*	0	200*	40*	35*	0	40*	725*
3 Aug	40*	50	0	0	60*	150*	0	X	40*
8 Aug	29	200*	0	0	24	45	0	X	120*
12 Aug	200*	0	0	90*	90*	200*	0	X	X
17 Aug	100*	8	0	75*	---	X	0	---	X
22 Aug	X	200*	5	25*	---	100*	0	84	---
31 Aug	250*	200*	40*	25	100	100	0	60*	140*
6 - 7 Sep	200*	100*	150*	25	26	150*	0	11	150*
13 Sep	---	---	39	---	---	---	0	---	---
18-19 Sep	---	---	---	100*	0	---	0	---	---
22-23 Sep	---	---	---	---	---	---	150*	---	14

Appendix 6.--Distances moved by desert tortoises between observations in 1993. Brackets indicate oviposition windows; dashes indicate undetermined movement distance (>0 m); X indicates tortoise not located on 1 July; asterisks indicate estimated distances. A series of zeros after oviposition indicates potential nest guarding.

Date	Distance moved (m)									
	01	04	12	17	18	19	21	33	13	14
12 Mar	10	30*	0	3	35	0	30*		0	0
23-24 Mar	10	50*	40*	29	22	200*	80*		75*	11
7- 8 Apr	48	80*	75*	75*	40*	0	26		100*	35
17 Apr	30*	30*	80*	50*	50*	0	60*		6	22
4 May	50*	50*	50*	13	50*	0	40*		90*	50*
19-20 May	0	60*	150*	40*	30*	35*	0		12*	0
6 Jun	25	30*	40	0	6	45*	100*		30*	0
12 Jun	0	30*	5	0	26	45*	300*		50*	17
19-20 Jun	0	100*	35	0	26	30*	0		---	200*
26-27 Jun	---	17	0	4	25*	0	0		29	75*
1 Jul	---	X	0	4	X	X	X		X	X
10-11 Jul	0	0	300*	50*	0	0	0	New	---	---
24-25 Jul	0	0	0	0	0	0	0	50*	---	---
7- 8 Aug	0	60*	0	0	0	0	50*	25*	40*	---
21-22 Aug	0	50*	0	0	0	0	50*	75*	---	---
11-12 Sep	40*	100*	>100	0	15	40*	4	300*	100*	---